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Relationships between habitat and recruitment of three species of damselfish (Pomacentridae) at Heron Reef, Great Barrier Reef

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Abstract

Recruitment of coral-reef fish species varies widely on a range of spatial scales, but the extent to which this variation is related to variability in habitat structure is unclear. We examined relationships between the recruitment of three species of damselfish (*Pomacentrus moluccensis* Bleeker, *P. wardi* Whitley and *P. amboinensis* Bleeker) and microhabitat structure (composition of the substrata) across six broad habitat zones at Heron Reef. Comparison of the distribution of recruits with the availability of substratum types along 10×2-m belt transects indicated that recruits of all three species utilised the substrata non-randomly. However, despite the distinct patterns of microhabitat use exhibited by each species, relationships between the density of recruits and the availability of preferred substrata were poor. We suggest that spatial stochasticity in larval supply and/or post-settlement mortality weakens relationships between recruitment and microhabitat availability. Univariate and multivariate analyses indicated significant differences in the recruitment of each species and in overall recruitment among habitat zones, and these differences may reflect large-scale variation in larval supply and/or rates of post-settlement mortality. Based on combined recruitment data, there was little evidence to suggest that areas of patchy coral reef received more or less recruitment than comparable areas of contiguous reef. Furthermore, recruitment to lagoonal patch reefs did not differ from recruitment to nearby sections of the reef slope offering a similar habitat with respect to depth and characteristics of the substratum. © 1998 Elsevier Science B.V.

Keywords: Coral reef fish; Habitat utilisation; Larval supply; Microhabitat structure; Post-settlement mortality; *Pomacentrus*; Recruitment

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1. Introduction

The life history of almost all benthic fish species on coral reefs includes a planktonic larval phase, which usually lasts from 3 to 6 wks (Johannes, 1978; Brothers et al., 1983; Thresher, 1984). Replenishment of adult populations occurs via settlement of these larvae, and recruitment is defined as the number of settled individuals which survive to some arbitrary time following larval settlement (Keough and Downes, 1982; Connell, 1985). Consequently, the dynamics of recruitment may be influenced by a range of physical and biological processes which act both prior to settlement and shortly following settlement (Levin, 1996). In the pre-settlement period, larvae drift pelagically and are subject to high and variable mortality (reviewed by Richards and Lindeman, 1987; Doherty and Williams, 1988; Sale, 1990; Booth and Brosnan, 1995). Similarly, for many species, mortality immediately following settlement is also high (Doherty and Sale, 1985; Shulman and Ogden, 1987; Sale and Ferrel, 1988; Levin, 1994; Carr and Hixon, 1995). Spatial and temporal heterogeneity in both pre- and post-settlement mortality has the potential to uncouple recruitment with the size of local spawning stocks, leading to high variability in recruitment at multiple scales (reviewed by Richards and Lindeman, 1987; Doherty and Williams, 1988; Doherty, 1991). Given the potential importance of recruitment in determining adult population size in coral reef fishes (see Doherty and Williams, 1988; Doherty and Fowler, 1994a,b), it is important that the underlying causes of recruitment variability are understood, particularly with respect to the relative importance of pre- and post-settlement processes (Munro and Williams, 1985).

A number of studies have documented a high degree of variability in reef fish recruitment over a range of spatial (10^1–10^5 m) and temporal scales (hours, days, years) (Russel et al., 1977; Williams and Sale, 1981; Victor, 1982, 1983, 1986; Williams, 1983; Eckert, 1984; Sale et al., 1984b; Sale, 1985; Schroeder, 1985; Shulman, 1985a; Doherty, 1987; Fowler et al., 1992; Planes et al., 1993; Doherty and Fowler, 1994a,b). Few, however, investigate the mechanisms underlying this variability. The extent to which fluctuations in recruitment are dependent on stochastic (e.g., oceanographic variation in larval supply) and/or deterministic processes (e.g., non-random habitat utilisation by recruits) remains unclear (see Milicich et al., 1992; Milicich and Doherty, 1994; Levin, 1994, 1996).

Recruits of a number of coral reef fish species exhibit distinct patterns of microhabitat use (Williams and Sale, 1981; Sale et al., 1984a; Shulman, 1984; Eckert, 1985; Booth, 1992; Wellington, 1992; Booth and Beretta, 1994; Tolimieri, 1995). Depending on the strength of recruit–habitat associations and the distribution and availability of preferred microhabitat, deterministic patterns of microhabitat use may strongly influence spatial variation in recruitment. Therefore, our first aim was to examine relationships between the recruitment of three damselfish species (*Pomacentrus moluccensis* Bleeker, *P. wardi* Whitley, and *P. amboinensis* Bleeker) and microhabitat structure (composition of the substrata) among a number of broad-scale habitat zones at Heron Reef, southern Great Barrier Reef. This was accomplished using two related approaches. First, we identified the patterns of microhabitat use exhibited by recruits of each species in relation to the availability of substratum types in each habitat zone. Second, we correlated the

availability of preferred microhabitat with the density of recruits, both within and among habitat zones.

The second aim of the study was to examine spatial variation in recruitment among habitat zones, which included patchy and contiguous coral reef located in the lagoon and on the reef slope. Many of the previous studies investigating recruitment of coral reef fishes have been conducted on small, isolated artificial or natural patch reefs located in coral reef lagoons (e.g., Russel et al., 1977; Williams and Sale, 1981; Eckert, 1984; Shulman, 1984, 1985a; Sale, 1985; Schroeder, 1985; Doherty and Fowler, 1994a,b). While lagoonal patch reefs offer a number of advantages for study (e.g., fish populations on isolated patch reefs are easy to survey and experimentally manipulate), there are two potential problems associated with investigating recruitment to this habitat. First, because of tidal fluctuations, intermittent larval flow over the reef crest may lead to lower levels of recruitment and/or higher spatial and temporal variability in recruitment to lagoonal habitats than to the outer reef slope. Second, the concentration of larvae in the water and the intensity of larval settlement may decrease in moving from the reef slope to the central lagoon as larvae encounter an appropriate settlement habitat (Milicich and Doherty, 1994).

While some studies have investigated recruitment to contiguous habitats on the reef slope, most of these have focussed on identifying large-scale regional variation in recruitment (Sale et al., 1984b; Doherty, 1987; Fowler et al., 1992). Few have simultaneously compared recruitment across a number of broad-scale habitat zones within a single reef, other than to demonstrate that spatial variability exists (e.g., Planes et al., 1993). Therefore, our goal was to quantitatively compare the recruitment of three species of damselfish across different habitat zones, including the lagoon and the reef slopes on the northern and southern sides of Heron Reef. In particular, we focussed on whether rates of recruitment differed between contiguous and patchy coral reef. During settlement, fish larvae may respond to both visual and olfactory cues in selecting suitable settlement habitat (Sweatman, 1988; Booth, 1992). Consequently, sensory signals may be associated more strongly with large sections of contiguous reef than small patch reefs, leading to variation in the stimuli for settlement (e.g., large sections of contiguous reef are more visible than small patch reefs and may be the source of stronger chemical signals). Differences in recruitment to contiguous and patch reef habitats may also result from differences in habitat choice. Larvae settling on small, isolated patch reefs may exhibit more generalised patterns of habitat selection given that the diversity of settlement habitat is generally less on small habitat patches than on large sections of contiguous reef (Ault and Johnson, in press). Overall, it is important that comparisons are made between recruitment to lagoonal patch reefs and sections of contiguous reef on the reef slope if the many studies of patch reefs are to be generalised more widely.

2. Methods

2.1. Study location and species

This study was conducted at Heron Reef (23°21′ S, 151°55′ E) in the Capricorn

Bunker Group, southern Great Barrier Reef. Heron Reef is a typical platform coral reef comprising a shallow lagoon surrounded entirely by an intertidal reef flat, reef crest and outer reef slope. The lagoon ranges in depth from 2–6 m at low tide and supports patchy outcrops of coral growth (patch reefs) surrounded by sand. On the southern side of Heron Reef, the outer reef slope is composed of large tracts of contiguous coral growth which range in depth from 1–18 m. On the northern side, much of the reef slope is contiguous in nature (1–15 m depth), but in some parts, the reef slope is largely composed of patch reefs at 8–12 m depth.

During April, 1995, we examined the spatial distribution of recruits (0 + individuals) of three damselfish species (*Pomacentrus moluccensis*, *P. wardi*, and *P. amboinensis*) to six different habitat zones: (1) southern reef slope (contiguous) at 3 m depth (SCS), (2) southern reef slope (contiguous) at 8 m depth (SCD), (3) northern reef slope (contiguous) at 3 m depth (NCS), (4) northern reef slope (contiguous) at 8 m depth (NCD), (5) northern reef slope (patchy) at 8 m depth (NPD), and (6) lagoonal patch reefs at 3 m depth (LPS) (Fig. 1). All three species chosen for study recruited to these habitat zones in sufficient numbers to obtain useful data. For each species, most settlement occurs between November and February. Thus, in our study, recruits represented newly settled individuals that had survived 3–6 months. The marked seasonality of settlement allowed us to distinguish unambiguously, recruits from older individuals (1 +) on the basis of body size. In each species, recruits are brightly coloured and readily identifiable to species.

2.2. Survey methods

In each habitat zone, recruitment and microhabitat were surveyed visually by the same

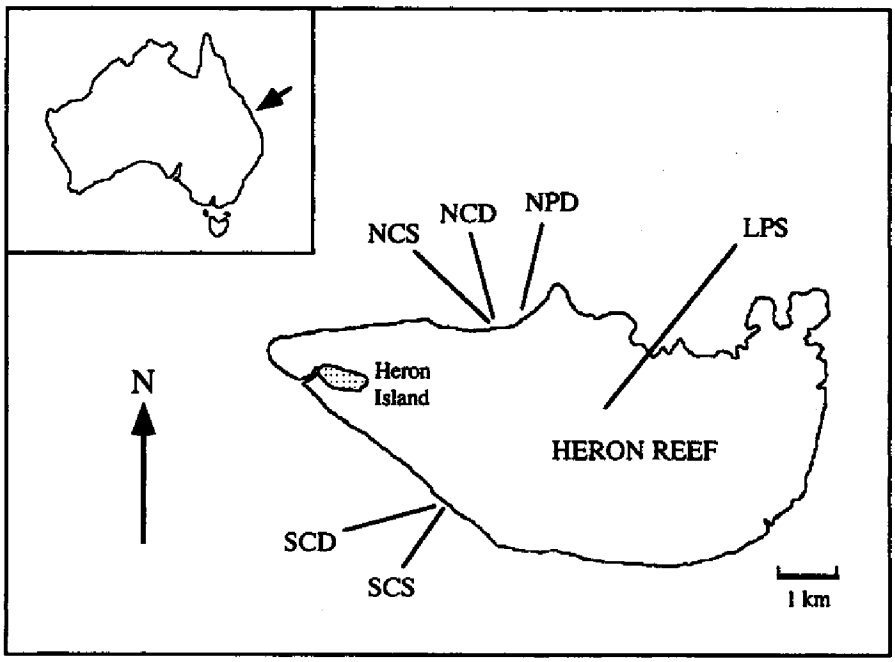

Fig. 1. Locations of habitat zones at Heron Reef. SCS = southern contiguous reef slope (shallow, 3 m depth); SCD = southern contiguous reef slope (deep, 8 m depth), NCS = northern contiguous reef slope (shallow); NCD = northern contiguous reef slope (deep); NPD = northern patchy reef slope (deep); LPS = lagoonal patch reefs (shallow).

diver (TRA) along 20 belt transects, each covering 10×2 m of reef (the exception was in the lagoon where only 17 transects could be completed). As belt transects in patchy reef zones included both reef and sand substrata, they were extended so that the area of reef surveyed was the same as on contiguous reef (10×2 m). Sections consisting entirely of sand contained no recruits of the target species and were not surveyed. During surveying, the number of recruits and the type of substratum directly below each individual recruit at the time it was first observed were recorded. Coral substrata were classified by growth form and included encrusting, digitate, branching, tabulate, massive and soft corals. Non-coral substrata included dead coral rock, rubble (fragments of coral rock < 5 cm in diameter) and sand (sand and fragments < 0.5 cm in diameter). During surveying, the diver hovered approximately 2 m above the substratum, descending only to count fish obscured by cover (e.g., under tabulate coral). Movement was kept to a minimum to avoid disturbing fish within the transect. Following surveying, the proportional composition of the reef substrata in each belt transect was estimated from a central line transect by measuring the combined length of line overlying each substratum type and dividing by the total length of reef surveyed (10 m).

2.3. Statistical analyses

2.3.1. Microhabitat utilisation by recruits

Patterns of microhabitat use by recruits of *P. moluccensis*, *P. wardi*, and *P. amboinensis* were assessed using the method outlined in Ault and White (1994). Separate analyses were conducted for each species in each habitat zone. To test for non-random microhabitat use, the number of recruits observed over each substratum category was compared to the number expected according to the proportional availability of that substratum type. Within each habitat zone, the mean percentage cover of each substratum category was calculated by averaging the results for the sample of 20 transects. For each substratum type, the expected number of recruits was calculated by multiplying the mean percentage cover by the total number of recruits observed. For example, if 25% of the area surveyed within a particular habitat zone comprised branching coral, then assuming no preferences in microhabitat use, 25% of all recruits surveyed should have been observed over branching coral. Frequency histograms of observed and expected numbers of recruits were plotted for each species in each habitat zone. To test for non-random microhabitat use, a χ^2 goodness-of-fit test was performed on the data for each species pooled across all habitat zones.

2.3.2. Relationships between microhabitat and recruit abundance

To examine relationships between the recruitment of each species and microhabitat structure, a habitat quality index (HQI) was used as an integrated measure of the suitability of individual transects with respect to the availability of preferred substrata. In the calculation of HQI for each transect, the proportional cover of each substratum type was multiplied by a weighting factor reflecting the degree of over- or under-representation in the observed number of recruits. For each species, separate weighting factors were calculated for each substratum category from data pooled across habitat zones by dividing the total number of recruits observed over that substratum type by the number

expected on the basis of substratum availability (i.e., if twice as many recruits occurred over branching coral than were expected based on non-selective microhabitat use, then branching coral would be weighted by a factor of 2). For convenience, these values were standardised to a maximum value of 1 by dividing by the maximum weighting factor. The habitat quality index (HQI) was then calculated for each transect as the sum of the weighted proportions of each substratum type, i.e.:

$$\mathrm{HQI} = \sum_{i=1}^{n} (P_n^* W_n)$$

where P_n = the proportional cover of the nth substratum type, and W_n is the weighting factor for the nth substratum type. An HQI value of zero would correspond to a transect comprising 100% of substrata over which no recruits were observed. An HQI value of 1 would correspond to a transect comprising 100% of the most favoured substratum type.

If levels of larval supply and rates of post-settlement mortality are spatially uniform over the area in which transects are located, spatial variability in the density of recruits should reflect variation in the availability of preferred microhabitat among transects. Thus, there should be a significant positive relationship between recruit density and HQI. However, high degrees of spatial variation in larval supply and/or post-settlement mortality may weaken relationships between recruitment and microhabitat structure. For each species, relationships between recruit density and HQI were evaluated by both Pearson correlation (r) and Spearman rank correlation (r_s). Spearman rank correlation was used in addition to r to indicate whether HQI could be used to rank transects in order of habitat quality if relationships between recruitment and HQI were non-linear. Significance of r and r_s was evaluated using one tailed tests as only positive correlations between recruit density and HQI were expected.

2.3.3. Differences in recruitment among habitat zones

After visual inspection of bivariate scatterplots and frequency histograms, data on recruitment were transformed to log $(X+1)$ to improve normality, linearity, and homogeneity of variance. For each species, a one-way ANOVA was conducted on transformed data to test for differences in the magnitude of recruitment among habitat zones. Following each ANOVA, total variance in recruitment was partitioned into variation among zones and variation within zones, expressed as percentages (Sokal and Rohlf, 1995, p. 214).

Differences in the combined recruitment of *P. moluccensis*, *P. wardi* and *P. amboinensis* among habitat zones were investigated using multivariate analysis of variance (MANOVA) with Pillai's trace (see Johnson and Field, 1993). Following MANOVA, variation in overall recruitment among zones was depicted by plotting the bivariate centroids of each group (with associated 95% confidence limits; see Sokal and Rohlf, 1995, pp. 586–593) in multivariate space using canonical discriminant analysis (CDA). Patterns revealed by the MANOVA and CDA were confirmed using cluster analysis which does not depend on the assumptions of linear modelling. Average linkage clustering was performed on a matrix of Bray Curtis similarities summarising variation

in the mean recruitment of each species among habitat zones (recruitment data transformed to $\log[X+1]$).

3. Results

3.1. Microhabitat utilisation by recruits

The substratum of the southern contiguous reef slope at both 3 and 8 m depth was characterised by high proportions of live coral (mainly encrusting and branching coral) and relatively low proportions of non-coral substrata (Table 1). In contrast, the northern contiguous reef slope and lagoonal patch reefs at 3 m depth were largely composed of dead coral rock with smaller proportions of rubble and sand (Table 1). The composition of the substrata was similar for both contiguous and patchy reef at 8 m on the northern reef slope.

Recruits of *P. moluccensis* displayed consistent patterns of microhabitat utilisation across all habitat zones examined (Fig. 2). In all zones, recruits were over-represented on digitate and branching coral and under-represented on other substrata, particularly on dead coral rock (Fig. 2). Due to the small samples sizes obtained from some habitat zones (e.g., northern contiguous reef at 3 m and lagoonal patch reefs), goodness-of-fit tests of observed versus expected distributions could not be performed on data obtained from each habitat zone (since calculated values of χ^2 are biased when expected frequencies are small; Zar, 1984). However, a χ^2 goodness-of-fit test on data pooled across all habitat zones (Fig. 2) indicated that the observed pattern of microhabitat use differed significantly from that expected on the basis of substratum availability ($\chi^2 = 4262.5$, d.f. $= 8$, $P = 0.0001$).

Pomacentrus wardi also showed consistent patterns of microhabitat use, with recruits over-represented on dead coral rock in all habitat zones except the northern contiguous

Table 1
Mean (±standard error) percentage cover of nine substratum types across six habitat zones on Heron Reef

Substratum type	Percentage cover					
	SCS	SCD	NCS	NCD	NPD	LPS
Encrusting coral	18.0±2.3	27.0±2.4	9.4±2.0	15.0±1.7	16.6±3.0	2.7±0.8
Digitate coral	11.0±1.8	10.7±1.1	3.4±0.7	3.2±0.3	4.6±0.9	1.8±0.6
Branching coral	21.9±3.9	21.1±2.8	2.5±1.0	7.7±1.9	8.7±3.3	4.3±0.6
Tabulate coral	5.3±1.4	1.8±0.5	0.4±0.2	1.0±0.5	0.8±0.7	0
Massive coral	4.6±1.0	4.6±0.7	3.3±0.8	3.6±0.6	14.2±2.5	0.3±0.2
Soft coral	0.6±0.2	6.2±2.6	1.1±0.6	3.4±0.3	4.8±1.4	0.6±0.3
Dead coral rock	34.6±3.0	16.3±2.5	69.5±3.1	38.9±2.4	33.5±3.7	72.9±2.8
Rubble	3.7±2.3	10.0±1.5	9.35±1.2	17.9±1.7	9.1±1.7	13.5±2.2
Sand	0.4±0.3	2.4±0.8	1.3±0.8	9.3±2.0	7.7±1.4	3.9±0.8

SCS = south contiguous reef (shallow 3 m); SCD = south contiguous reef (deep 8 m); NCS = north contiguous reef (shallow); NCD = north contiguous reef (deep); NPD = north patchy reef (deep); LPS = lagoonal patchy reef (shallow).

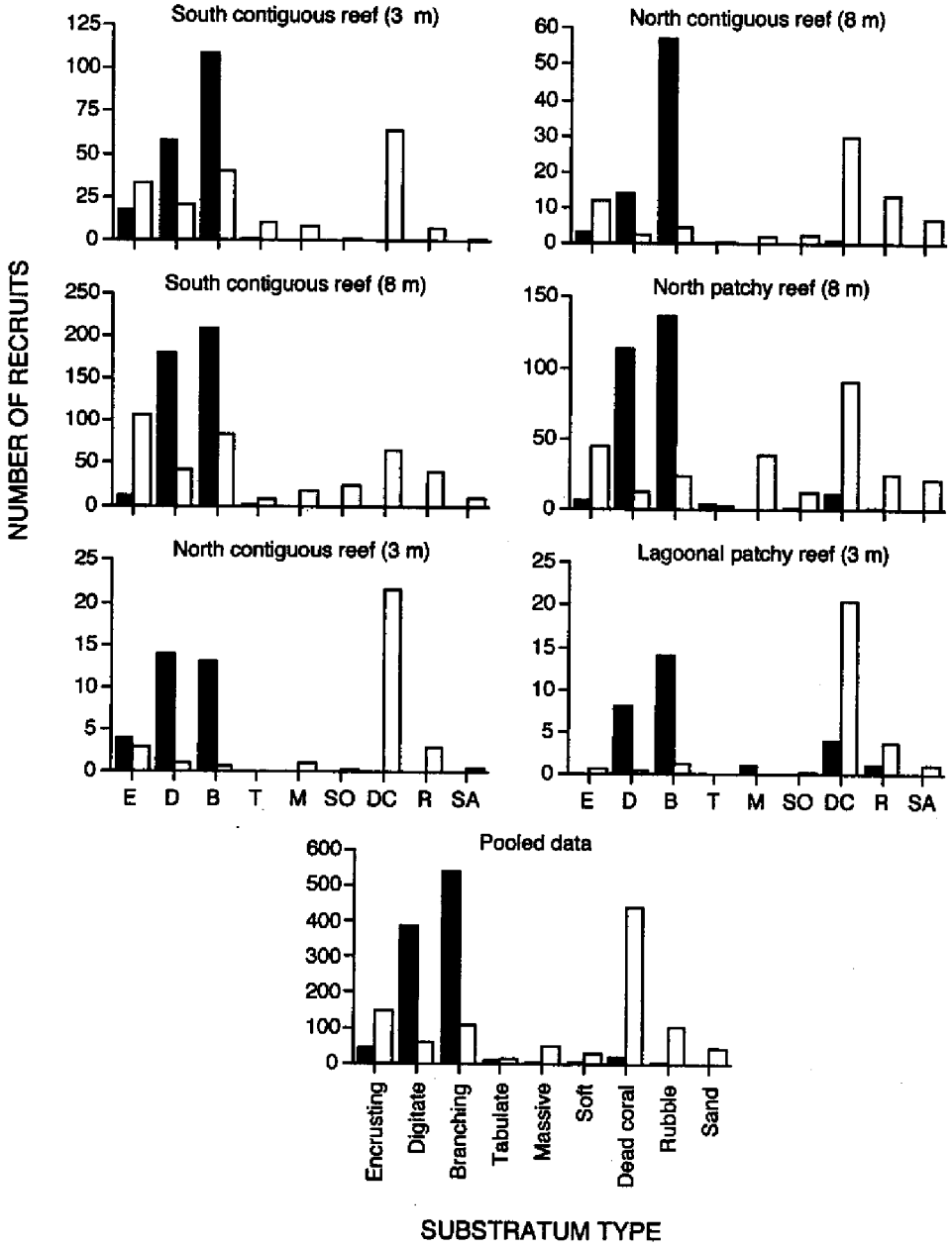

Fig. 2. Utilisation of the substrata by recruits of *Pomacentrus moluccensis* in each habitat zone. Dark bars indicate the number of recruits observed over each substratum type. Light bars indicate the number of recruits expected over each substratum type on the basis of proportional availability (see Section 3.1).

reef at 3 m depth (NCS) and the lagoonal patch reefs (LPS) (Fig. 3). In the latter habitat zones, recruits utilised dead coral rock, the most abundant substrata, in proportion with its availability (Fig. 3). A χ^2 goodness-of-fit test on pooled data (Fig. 3) indicated that recruits of *P. wardi* utilised microhabitat non-randomly ($\chi^2 = 80.6$, d.f. $= 8$, $P = 0.0001$).

Recruits of *P. amboinensis* were distributed more widely among substratum types than either *P. moluccensis* or *P. wardi* (Fig. 4). On the southern contiguous reef slope (SCS and SCD) and the contiguous and patchy reef at 8 m on the northern reef slope (NCD and NPD), recruits were observed primarily over digitate or branching coral, or dead coral rock or rubble (Fig. 4). On the northern contiguous reef slope at 3 m (NCS) and on lagoonal patch reefs (LPS), where low proportions of digitate and branching coral were available and few recruits were observed, recruits were mainly distributed over non-coral

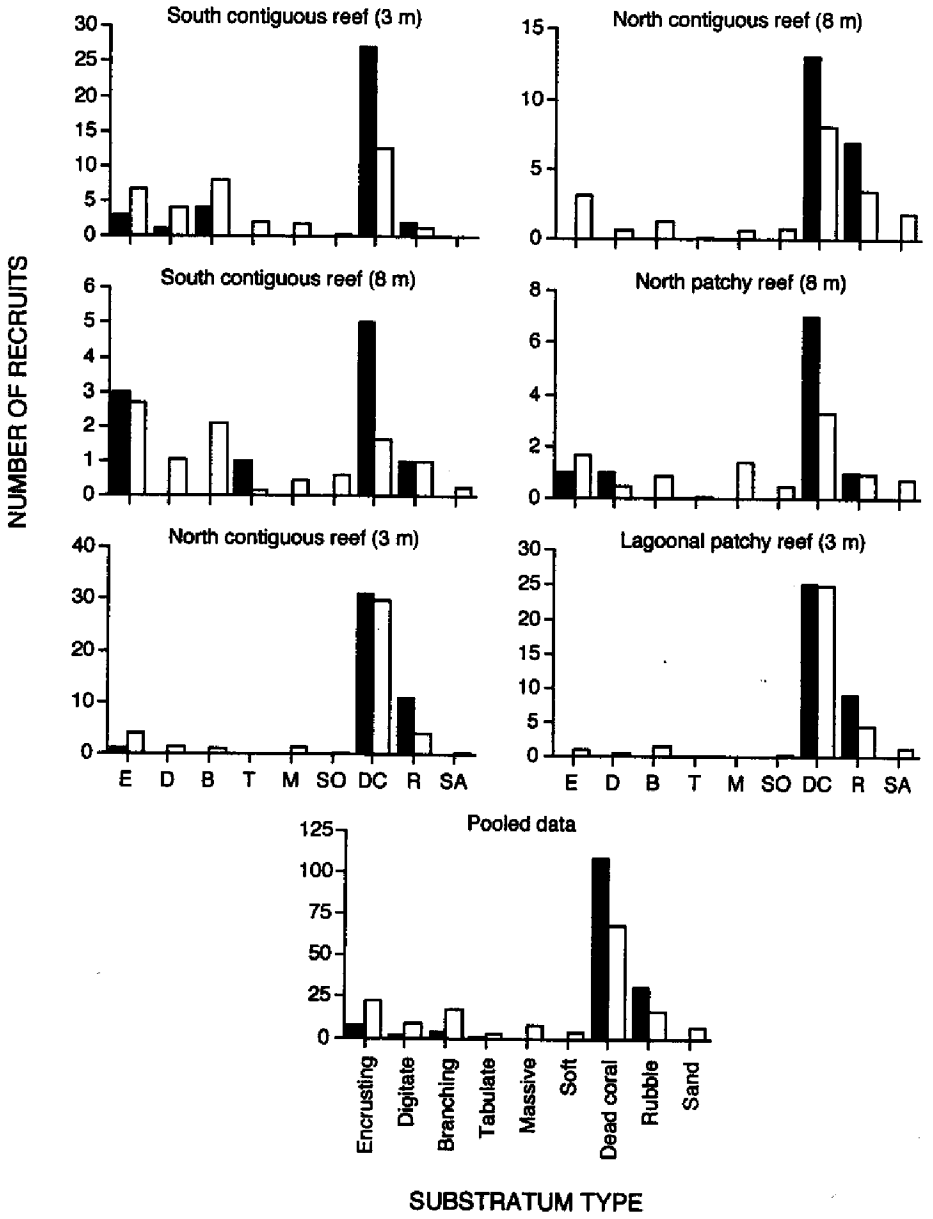

Fig. 3. Utilisation of the substrata by recruits of *Pomacentrus wardi* in each habitat zone. Dark bars indicate the number of recruits observed over each substratum type. Light bars indicate the number of recruits expected over each substratum type on the basis of proportional availability (see Section 3.1).

substrata (Fig. 4). Over all habitat zones (pooled data; Fig. 4), recruits of *P. amboinensis* were distributed non-randomly ($\chi^2 = 367.6$, d.f. $= 8$, $P = 0.0001$).

3.2. Relationships between spatial variability in recruitment and microhabitat structure

Despite the clear and consistent patterns of habitat utilisation displayed by all three damselfish species (Figs. 2–4), densities of recruits were poorly correlated with the availability of preferred habitat (HQI values for each species) at the scale of transects within habitat zones (Table 2). In the analysis, calculation of HQI on the basis of pooled data was justified given the consistent habitat preferences exhibited by recruits of each

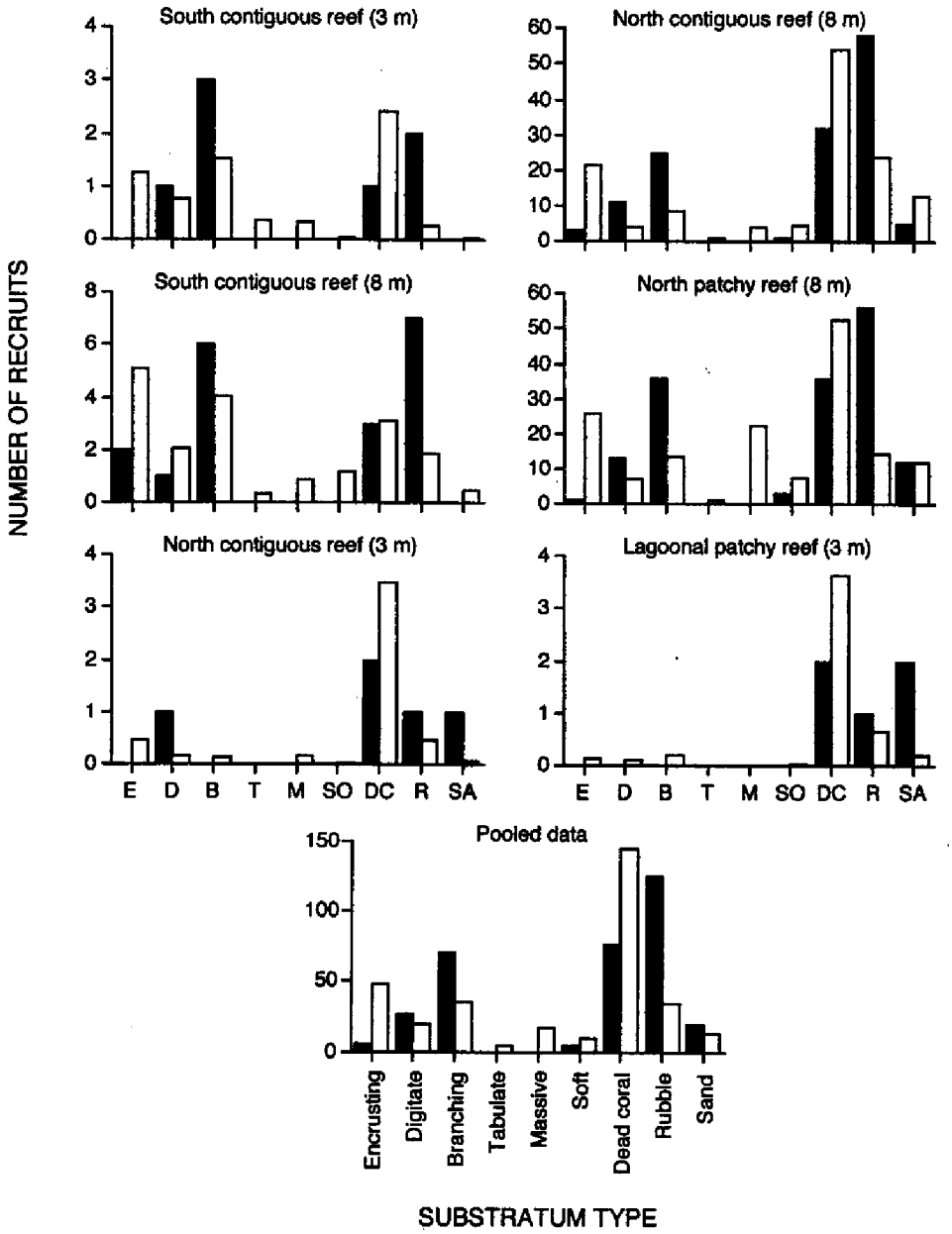

Fig. 4. Utilisation of the substrata by recruits of *Pomacentrus amboinensis* in each habitat zone. Dark bars indicate the number of recruits observed over each substratum type. Light bars indicate the number of recruits expected over each substratum type on the basis of proportional availability (see Section 3.1).

species regardless of variation in the availability of different substrata among habitat zones (Table 1 Figs. 2–4).

For *P. moluccensis* and *P. wardi*, there were no linear relationships between the density of recruits and HQI within habitat zones (Pearson's r; Table 2). For *P. amboinensis*, recruit density was correlated with HQI only on the southern reef slope (SCS and SCD; Table 2) where recruit density was very low (Fig. 5). When HQI was used to rank transects according to habitat suitability, Spearman rank correlations (r_s) were not-significant for all but 5 of the 18 cases (Table 2). Among habitat zones (i.e., pooling data from all transects), there were significant but weak correlations between the density of recruits and HQI for all three species (Fig. 6). Overall, at the scale of

Table 2
Pearson correlation (r) and Spearman rank correlation (r_s) between recruit density and HQI for transects within six habitat zones

Habitat	*P. moluccensis*		*P. wardi*		*P. amboinensis*	
	r	r_s	r	r_s	r	r_s
SCS	0.001	−0.094	0.073	0.273	0.703[a]	0.247
SCD	0.122	0.183	0.086	0.041	0.528[a]	0.503[a]
NCS	0.248	0.117	−0.120	−0.170	−0.058	0.010
NCD	0.205	0.289	0.199	0.248	0.326	0.408[a]
NPD	0.294	0.532[a]	−0.016	−0.060	0.318	0.601[a]
LPS	0.368	0.456[a]	0.411	0.335	0.103	0.033

SCS = south contiguous reef (shallow 3 m); SCD = south contiguous reef (deep 8 m); NCS = north contiguous reef (shallow); NCD = north contiguous reef (deep); NPD = north patchy reef (deep); LPS = lagoonal patchy reef (shallow). Significance based on one-tailed tests; $n = 20$, except for LPS where $n = 17$ (see Section 3.2).
[a] $P < 0.05$.

transects, HQI was a poor predictor of recruit density, both within and among habitat zones.

3.3. Variation in recruitment among habitat zones

For each of the three species examined, there were significant differences in recruitment among habitat zones (Table 3). For *P. moluccensis*, approximately 70% of total variation in recruitment was due to differences in recruit density among habitat zones, while differences among transects within zones accounted for the remaining 30% (Table 3). Densities of *P. moluccensis* recruits were highest on the southern contiguous reef slope at 8 m (SCD) and on the northern patchy reef slope at 8 m depth (NPD) (Fig. 5). Recruits of *P. wardi* were more evenly distributed among habitat zones (Fig. 5), and consequently, most variation in recruitment was due to differences among transects within zones (74%; Table 3). For *P. amboinensis*, among- and within-zone components of variation contributed 60% and 40% of total variability in recruitment respectively (Table 3). Recruits of *P. amboinensis* were found most commonly at 8 m depth on the northern slope irrespective of whether the reef was contiguous or fragmented into distinct patches (NCD and NPD) (Fig. 5).

A one-way MANOVA indicated significant differences in overall recruitment among habitat zones (Pillai's trace = 1.317; $F = 17.364$; d.f. = 15, 333; $P < 0.0001$). In a canonical discriminant analysis, most between-group variability was explained by the first two canonical axes (72.4% and 26.7% respectively; calculated from eigenvalue magnitude). The analysis indicated that recruitment to the northern contiguous reef slope at 3 m depth (NCS) and to lagoonal patch reefs (LPS) were similar, but for the other habitat zones, there was some separation along both canonical axes (Fig. 7).

The dendrogram obtained from average-linkage clustering of mean recruitment data divided the habitat zones into three groups based on recruitment of all three species (Fig. 8). In addition to the northern contiguous reef slope at 3 m (NCS) and lagoonal patch

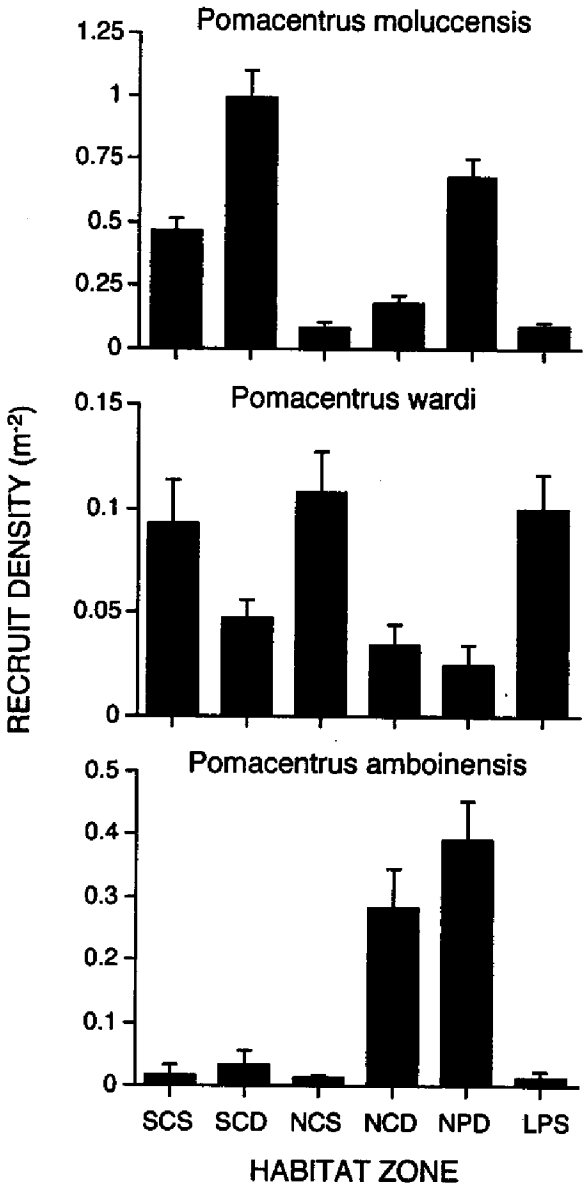

Fig. 5. Mean density of recruits estimated from 20 transects (17 for LPS) in each habitat zone. SCS = southern contiguous reef slope (shallow, 3 m depth); SCD = southern contiguous reef slope (deep, 8 m depth); NCS = northern contiguous reef slope (shallow); NCD = northern contiguous reef slope (deep); NPD = northern patchy reef slope (deep); LPS = lagoonal patch reefs (shallow).

reefs (LPS), the two habitat zones on the southern contiguous reef slope (SCS and SCD) were clustered together, as were the habitat zones at 8 m on the northern reef slope (NCD and NCP) (Fig. 8). These groupings reflected the proximities of bivariate centroids and the overlap in data polygons in the canonical discriminant ordination (Fig. 7).

4. Discussion

4.1. Microhabitat utilisation by recruits

A number of previous studies have demonstrated that recruitment of many reef fish

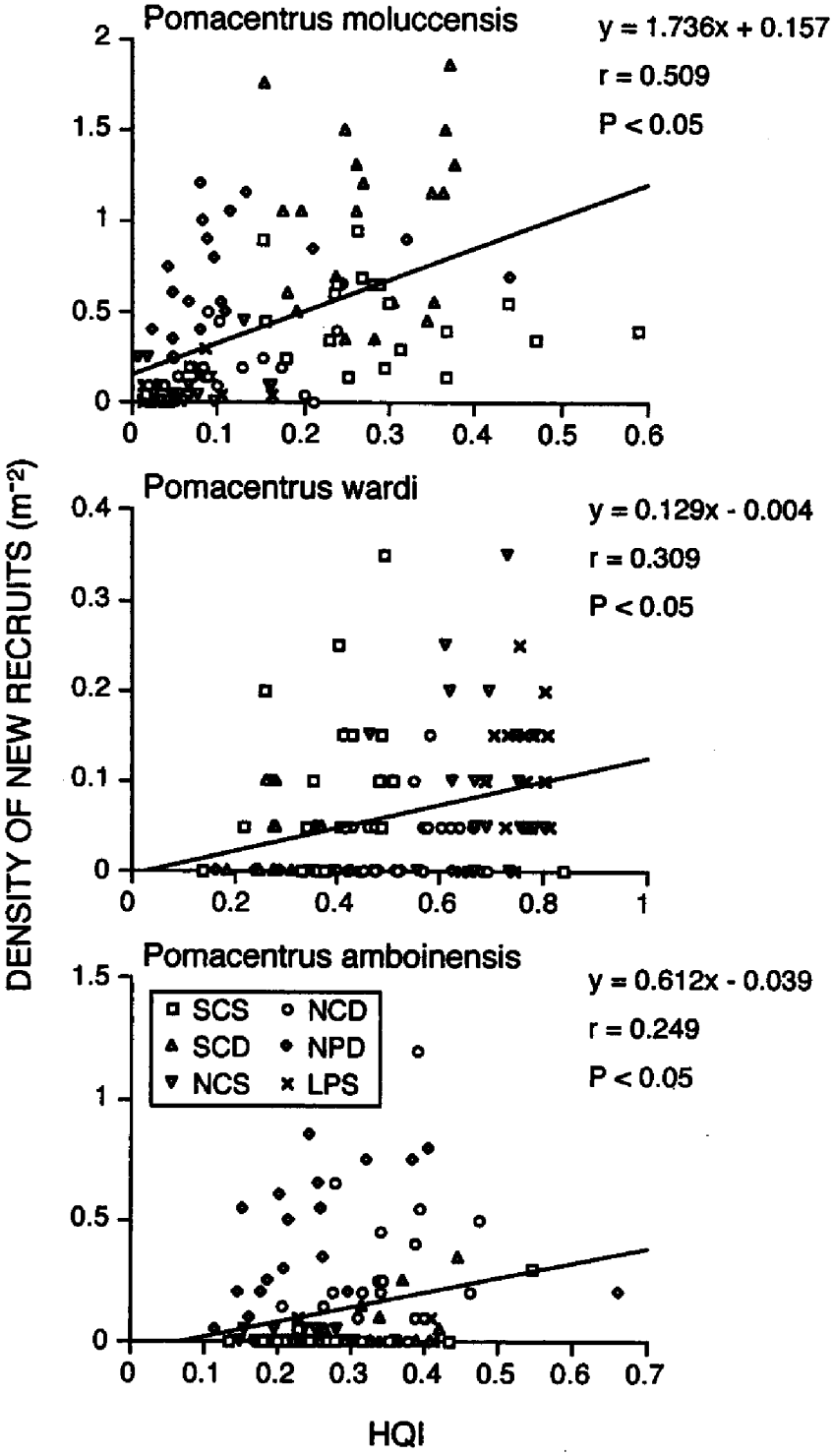

Fig. 6. Relationship between the density of recruits and HQI for data pooled across all habitat zones. Significance based on one-tailed tests.

species in both temperate and tropical environments is influenced by habitat structure (Williams and Sale, 1981; Sale et al., 1984a; Shulman, 1984; Eckert, 1985; Carr, 1991; Levin, 1991, 1993; Booth, 1992; Wellington, 1992; Booth and Beretta, 1994; Tolimieri, 1995). Similarly, recruits of the three species of damselfish investigated in our study exhibited non-random patterns of microhabitat use. Recruits of *P. moluccensis* were consistently positioned over branching or digitate coral, while recruits of *P. wardi* were distributed almost exclusively over dead coral rock or rubble substrata. *Pomacentrus*

Table 3
Results of one-way ANOVAs testing variation in recruitment among habitat zones for *P. moluccensis*, *P. wardi* and *P. amboinensis*

Source of variation	d.f.	MS	*F*	*P*	Percent of variation
P. moluccensis					
Among zones	5	17.90	47.79	<0.001	70.6
Within zones	111	0.38	–	–	29.4
P. wardi					
Among zones	5	2.16	7.73	<0.001	25.7
Within zones	111	0.28	–	–	74.3
P. amboinensis					
Among zones	5	12.43	29.80	<0.001	59.6
Within zones	111	0.42	–	–	40.4

Percent of variation among zones and within zones is also given (see Section 3.3).

amboinensis appeared more flexible in the use of microhabitat, occurring commonly over dead coral rock or rubble, or among the interstices provided by digitate and branching coral. In the majority of cases where recruits of *P. amboinensis* were found over live coral, non-coral substrata was situated nearby, and *vice versa*. From our observations of this species, it appeared that digitate and branching coral were used mainly for shelter, while non-coral substrata were used for feeding and social interactions.

For the three fish species examined in our study and for *P. moluccensis* in particular, patterns of microhabitat use by recruits were consistent among habitat zones despite

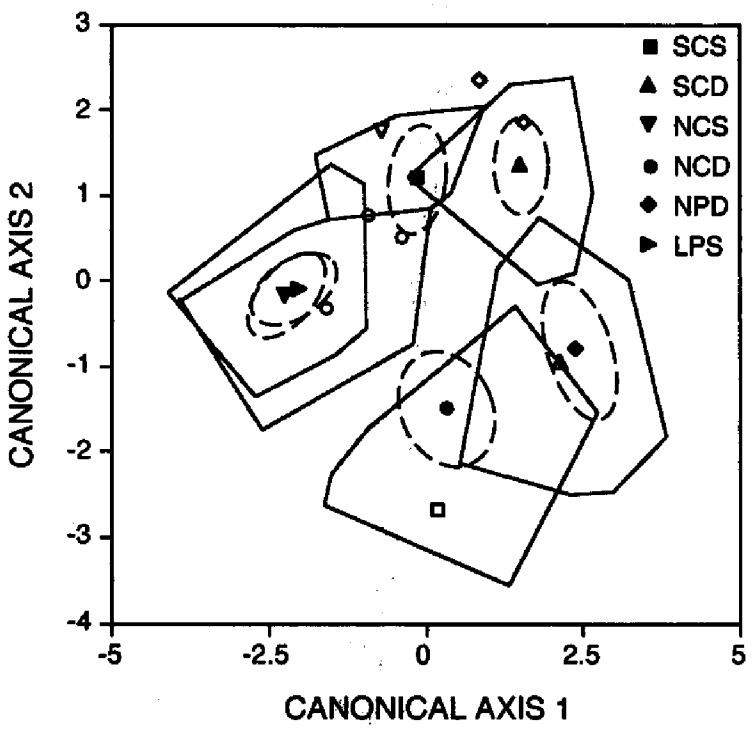

Fig. 7. Ordination of habitat zones using canonical discriminant analysis of recruitment of all three fish species. Bivariate centroids (closed symbols) and associated 95% confidence ellipses (dashed lines) are shown along with polygons enclosing all transects within zones (extreme outliers indicated by open symbols).

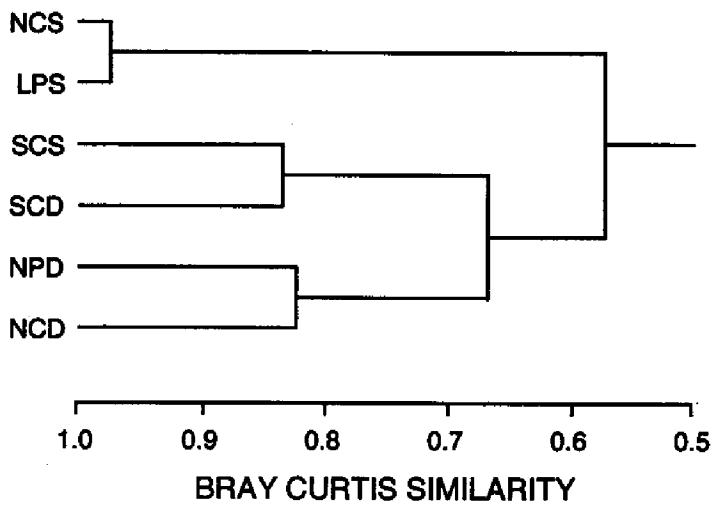

Fig. 8. Average-linkage cluster dendrogram summarising the similarity (Bray Curtis) of mean recruitment of all species among habitat zones.

marked differences in the composition of the substrata. There was slight variation in the patterns of microhabitat use exhibited by recruits of *P. wardi* and *P. amboinensis* on the north contiguous reef at 3 m (NCS) and on lagoonal patch reefs (LPS) relative to other habitat zones. For *P. amboinensis*, utilisation of digitate and branching coral was lower in these habitat zones than in others. However, the availability of both substratum types was very low in both NCS and LPS, and observed patterns of microhabitat use were based on only a small number of observations in both zones. For *P. wardi*, recruits were distributed in accordance with the availability of dead coral rock in NCS and LPS, while being over-represented on this substratum type in other habitat zones. These differences probably reflect the high availability of dead coral rock in NCS and LPS. Even if a species has an obligate requirement for a particular substratum type and utilises no other substrata, the ratio of observed to expected numbers will tend towards 1:1 as the availability of the preferred substrata approaches 100% cover.

There are a number of possible explanations for the distinct patterns of microhabitat use exhibited by the recruits of each species. First, the distribution of recruits may be established by substratum choice during settlement. Second, settlement may be unaffected by habitat availability, but differences in mortality rates among substratum types for different species may result in the observed patterns of microhabitat use. For example, mortality for individuals of *P. moluccensis* settling on dead coral rock may be much higher than that for individuals settling on digitate or branching coral. Manipulative experimentation by other workers suggests that for recruits of coral reef fish species, non-random utilisation of substrata is more likely the result of active microhabitat selection during settlement rather than differential survival among habitat types following settlement (Booth, 1992; Wellington, 1992; Tolimieri, 1995).

A third possibility is that patterns of microhabitat use by recruits may reflect the movement of individuals shortly following settlement. Larvae may settle randomly over the reef but may relocate according to habitat preferences or in response to the densities of predators or competitors. In another study (Ault and Johnson, in press), we found that for the damselfish species examined here, relationships between total population density

(i.e., recruits and adults) and habitat structure were stronger on contiguous reef than on patchy reef. We argued that this result may reflect the enhanced opportunities for site-attached fish species on contiguous reef to relocate following settlement. Holes and coral interstices on contiguous reef provide refuge from predators in all directions, while on isolated patch reefs, migrating individuals must cross open stretches of sand where there is little or no protection from predation. In the present study, patterns of microhabitat use displayed by recruits were similar regardless of whether the reef was patchy (NPD and LPS) or contiguous in nature (SCS, SCD, NCS, and NCD). This result is consistent with the experimental studies which suggest that the patterns of microhabitat use displayed by new recruits are established at settlement (Booth, 1992; Wellington, 1992; Tolimieri, 1995).

4.2. Relationships between spatial variability in recruitment and microhabitat structure

For each of the species examined, recruits exhibited consistent patterns of non-random microhabitat use among habitat zones, suggesting possible relationships between the densities of recruits and the availability of preferred habitat (as reflected by HQI). However, relationships between recruitment and microhabitat structure were either not-significant or only weakly significant both within and among habitat zones. Within zones, there were very few significant relationships (linear or rank correlation) between recruit density and HQI. Transects containing a high proportion of the substratum preferred by recruits did not necessarily support higher densities of recruits. Similarly, when data were pooled across all habitat zones, relationships between recruitment and HQI were weak (albeit significant), characterised by a high degree of scatter around the fitted line (Fig. 6).

There are a number of possible explanations for the poor relationships between recruitment and habitat structure despite the distinct patterns of microhabitat use exhibited by recruits of all three species. First, spatial heterogeneity in larval supply over the scale at which transects were located may have weakened predictable relationships between recruitment and the availability of preferred habitat. This hypothesis is supported by Doherty (1987) who suggested that small-scale patchiness in larval abundance may explain the high spatial variability in recruitment to replicate patch reefs separated by tens of meters. Spatial heterogeneity in larval supply could arise from physical (e.g., hydrodynamic variability) and/or biological processes (e.g., aggregation of larvae prior to settlement; see Breitburg, 1989, 1991).

Second, relationships between recruitment and microhabitat structure may be disrupted by spatial variability in rates of post-settlement mortality. A number of studies have indicated that regimes of post-settlement mortality, and in particular losses to predation, can profoundly affect the distribution and abundance of coral reef fishes (Hixon, 1991; Hixon and Beets, 1993; Carr and Hixon, 1995). While predation pressure may reinforce patterns of microhabitat selection during settlement (Wellington, 1992; Tolimieri, 1995), spatial and temporal heterogeneity in the magnitude of predation has the potential to modify patterns established at settlement and weaken relationships between recruitment and microhabitat availability (Alderhoven, 1986; Eckert, 1987;

Shulman and Ogden, 1987; Hixon, 1991). Both predator abundance and rates of mortality may vary widely within and among habitat zones on coral reefs (Kingsford, 1992; Connell, 1996, 1997).

Third, it might be argued that for each of the species examined, rates of larval settlement were insufficient to saturate available microhabitats, resulting in poor relationships between recruitment and HQI. However, in some habitat zones, recruitment was very high, particularly for *P. moluccensis* on the southern reef slope at 8 m depth (SCD). If relationships between recruitment and habitat were reliant on habitat saturation, we might expect correlations (linear and/or rank) between the density of recruits and HQI to increase with the magnitude of recruitment. In no species was this pattern evident, with the possible exception of *P. amboinensis*. For this species, rank correlations were significant for NCD and NPD where recruitment was highest, but also for SCD where recruitment was very low.

Finally, it is possible that the poor relationships between recruitment and HQI were due to differences in the spatial scale of the various statistical analyses (Morris, 1987). Calculations of HQI were based on weighting factors (W) derived from analyses of microhabitat utilisation by recruits of each species. Due to the small samples sizes obtained for some species in some habitat zones, analyses of microhabitat use were conducted on transect data pooled across all habitat zones. In contrast, HQI values were used to indicate the availability of preferred habitat at the scale of individual transects. Despite this difference in scale, significant relationships between the density of recruits and HQI might still be expected provided that analyses of habitat preferences are consistent among habitat zones and independent of spatial scale. Given the uniformity of the analyses of microhabitat use among habitat zones and pooled data for each species (Figs. 3–5), there is little evidence to indicate transgression of these criteria. Thus, we suggest that the weak relationships between recruitment and habitat structure are unlikely to be a scale-dependent artefact and are most likely due to spatial stochasticity in larval supply and/or post-settlement mortality.

4.3. Differences in recruitment among habitat zones

There was significant variation in the recruitment of each species and in overall recruitment among habitat zones. Spatial variability in recruitment and the distribution of larvae among habitat zones has also been reported by other researchers (Milicich et al., 1992; Planes et al., 1993; Milicich, 1994; Milicich and Doherty, 1994; Doherty et al., 1996). At Lizard Island, Milicich and Doherty (1994) observed a reduction in the density of late-stage larvae of some fish species in lagoonal water compared to water off the reef slope. However, for the three species examined at Heron Reef, there was very little difference between the overall recruitment to patch reefs in the lagoon and to contiguous reef located at 3 m along the northern reef slope. As the depth and characteristics of the substratum of both habitats are similar, there is little evidence to suggest that the periodic isolation of the Heron Reef lagoon at low tide results in lower or more variable rates of recruitment to lagoonal patch reefs than to the northern reef slope at similar depths.

The correspondence in overall recruitment to lagoonal patch reefs and the northern

contiguous reef slope at 3 m, and the similarity in recruitment to the patchy and contiguous northern reef slope at 8 m, suggest that recruitment rates are comparable between patchy and contiguous coral reef. A number of studies have assessed the effects of patch size and isolation on recruitment (Molles, 1978; Walsh, 1985; Schroeder, 1987). However, these studies have focussed largely on identifying responses to the size and connectivity of individual patch reefs. Few studies have compared recruitment to large areas of patchy reef with that to equivalent areas of contiguous reef. Our study suggests that measurements of recruitment taken from patch reefs can be generalised to nearby contiguous reef habitats, at least for the study species at Heron Reef.

There are a number of possible reasons for the differences in recruitment among habitat zones revealed in our study. These can be divided into two broad categories based on processes that; (1) affect the distribution and abundance of larvae prior to settlement, and (2) modify patterns established at settlement. A number of studies have identified relationships between spatial and temporal variation in larval supply and the intensity of subsequent recruitment (Milicich et al., 1992; Milicich, 1994; Milicich and Doherty, 1994). However, the causal mechanisms underlying spatial variation in larval density remain unclear. The distribution and abundance of larvae prior to settlement may be influenced by broad-scale habitat selection among zones. This notion is consistent with the classification of habitat zones into three groups, based on overall recruitment (Fig. 8), which were in general agreement with similarities in habitat characteristics (Table 1). Little is known about the sensory capabilities and behaviour of larval reef fish (Leis, 1991), but Milicich and Doherty (1994) and Doherty et al. (1996) provide evidence of large-scale habitat selection by reef fish larvae prior to settlement.

Differences in recruitment among habitat zones may also stem from spatial variation in larval supply. Hydrodynamic variability in the waters surrounding coral reefs can cause complex patterns of larval retention and transport (Leis, 1986; Leis and Goldman, 1987; Fowler et al., 1992; Milicich et al., 1992; Milicich, 1994; Milicich and Doherty, 1994; Wolanski, 1994). This variability, coupled with variations in larval biology and life history (e.g., spawning time, larval duration and/or larval behaviour) may lead to spatial and temporal differences in larval supply and recruitment among species (see Sponaugle and Cowen, 1996). In our study, the relative magnitudes of recruitment to each habitat zone differed among the species examined.

Variability in recruitment among habitat zones may also reflect spatial variation in the rates of post-settlement mortality among zones (Shulman, 1985b; Hixon and Beets, 1989, 1993; Hixon, 1991). Mortality of newly settled individuals is highest immediately following settlement (Victor, 1986; Sale and Ferrel, 1988; Carr and Hixon, 1995). At Heron Reef, the majority of settlement in the three species we examined occurs between November and February. Thus, in the time between settlement and recruitment (as recorded in this study), there was considerable potential for the modification of original settlement patterns by post-settlement processes, in particular by predation. Kingsford (1992) identified considerable variation in both the distribution and abundance, and feeding habits of predatory coral trout (*Plectropomus leopardus*) among habitat zones at nearby One Tree Reef on the southern Great Barrier Reef. At the same reef, Connell (1996), (1997) documented among-zone variation in both predator abundance and rates of mortality of a juvenile damselfish. Even if rates of larval settlement were spatially

homogeneous, differential rates of post-settlement mortality has the potential to uncouple settlement and recruitment, leading to spatial variability in recruitment among zones.

For the three species of damselfish examined in our study, the spatial dynamics of recruitment appears to be influenced by both deterministic and stochastic processes. While recruits of each species exhibit distinct patterns of microhabitat use, it is likely that small-scale patchiness in larval supply and/or post-settlement mortality transcends predictability in habitat utilisation, leading to unpredictable variation in the distribution and abundance of recruits at the scale of transects (both within and among habitat zones). Similarly, spatial variation in overall recruitment among habitat zones may be the result of deterministic and stochastic processes operating both before and after settlement. Further work is required to quantify the relative importance of spatial variability in larval supply, settlement and post-settlement mortality in determining spatial variation in recruitment over a range of scales.

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References

Alderhoven, J.M., 1986. Local variation in mortality rates and life-expectancy estimates of the coral reef fish Centropyge bicolor (Pisces: Pomacanthidae). Mar. Biol. 92, 237–244.

Ault, T.R., Johnson, R.C., in press. Spatially and temporally predictable fish communities on coral reefs. Ecol. Monogr.

Ault, T.R., White, R.W.G., 1994. Effects of habitat structure and presence of brown trout on the population density of *Galaxias truttaceus* in Tasmania, Australia. Trans. Am. Fish. Soc. 123, 939–949.

Booth, D.J., 1992. Larval settlement and preferences by domino damselfish *Dascyllus albisella* Gill. J. Exp. Mar. Biol. Ecol. 155, 85–104.

Booth, D.J., Beretta, G.A., 1994. Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. Coral Reefs 13, 81–89.

Booth, D.J., Brosnan, D.M., 1995. The role of recruitment dynamics in rocky shore and coral reef communities. Adv. Ecol. Res. 26, 309–385.

Breitburg, D.L., 1989. Demersal schooling prior to settlement by larvae of the naked goby. Env. Biol. Fish. 26, 97–103.

Breitburg, D.L., 1991. Settlement patterns and presettlement behaviour of the naked goby *Gobiosoma bosci*, a temperate oyster reef fish. Mar. Biol. 109, 213–221.

Brothers, E.B., Williams, D.McB., Sale, P.F., 1983. Length of larval life in twelve families of fishes at 'One Tree Lagoon', Great Barrier Reef, Australia. Mar. Biol. 76, 319–324.

Carr, M.H., 1991. Habitat selection and recruitment of an assemblage of temperate zone reef fishes. J. Exp. Mar. Biol. Ecol. 146, 113–137.

Carr, M.H., Hixon, M.A., 1995. Predation effects on early post-settlement survivorship of coral reef fishes. Mar. Ecol. Prog. Ser. 124, 31–42.

Connell, J.H., 1985. The consequences of variation in initial vs. post-settlement mortality in rocky intertidal communities. J. Exp. Mar. Biol. Ecol. 93, 11–45.

Connell, S.D., 1996. Variations in mortality of a coral-reef fish: links with predator abundance. Mar. Biol. 126, 347–352.

Connell, S.D., 1997. The relationship between large predatory fish and recruitment and mortality of juvenile coral reef-fish on artificial reefs. J. Exp. Mar. Biol. Ecol. 209, 261–278.

Doherty, P.J., 1987. The replenishment of populations of coral reef fishes, recruitment surveys, and the problems of variability manifest on multiple scales. Bull. Mar. Sci. 41, 411–422.

Doherty, P.J., 1991. Spatial and temporal patterns in recruitment. In: Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, pp. 261–293.

Doherty, P.J., Fowler, A., 1994a. An empirical test of recruitment limitation in a coral reef fish. Science 263, 935–939.

Doherty, P.J., Fowler, A., 1994b. Demographic consequences of variable recruitment to coral reef fish populations: a congeneric comparison of two damselfishes. Bull. Mar. Sci. 54, 297–313.

Doherty, P.I., Kingsford, M., Booth, D., Carleton, J., 1996. Habitat selection before settlement by *Pomacentrus coelestris*. Mar. Freshw. Res. 47, 391–399.

Doherty, P.J., Sale, P.J., 1985. Predation on juvenile coral reef fishes: an exclusion experiment. Coral Reefs 4, 225–234.

Doherty, P.J., Williams, D.McB., 1988. The replenishment of coral reef fish populations. Oceanogr. Mar. Biol. Annu. Rev. 26, 487–551.

Eckert, G.J., 1984. Annual and spatial variation in recruitment of labroid fishes among seven reefs in the Capricorn/Bunker Groups, Great Barrier Reef. Mar. Biol. 78, 123–127.

Eckert, G.J., 1985. Settlement of coral reef fishes to different natural substrata and at different depths. Proc. 5th Int. Coral Reef Congr. 5, 385–390.

Eckert, G.J., 1987. Estimates of adult and juvenile mortality for labrid fishes at One Tree Reef, Great Barrier Reef. . Mar. Biol. 95, 167–171.

Fowler, A.J., Doherty, P.J., Williams, D.McB., 1992. Multi-scale analysis of recruitment of a coral reef fish on the Great Barrier Reef. Mar. Ecol. Prog. Ser. 82, 131–141.

Hixon, M.A., 1991. Predation as a process structuring coral reef fish communities. In: Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, pp. 294–328.

Hixon, M.A., Beets, J.P., 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. Bull. Mar. Sci. 44, 666–680.

Hixon, M.A., Beets, J.P., 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecol. Monogr. 63, 77–101.

Johannes, R.E., 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fishes 3, 65–84.

Johnson, C.R., Field, C.A., 1993. Using fixed-effects model multivariate analysis of variance in marine biology and ecology. Oceanogr. Mar. Biol. Annu. Rev. 31, 177–221.

Keough, M.J., Downes, B.J., 1982. Recruitment of marine invertebrates: the role of active larval choice and early mortality. Oecologia 54, 348–352.

Kingsford, M.J., 1992. Spatial and temporal variation in predation on reef fishes by coral trout (*Plectropomus leopardus* Serranidae). Coral Reefs 11, 193–198.

Leis, J.M., 1986. Vertical and horizontal distributions of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. . Mar. Biol. 90, 505–516.

Leis, J.M., 1991. The pelagic stage of reef fishes: the larval biology of coral reef fishes. In: Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs, Academic Press, San Diego, pp. 183–230.

Leis, J.M., Goldman, B., 1987. Composition and distribution of larval fish assemblages in the Great Barrier Reef lagoon near Lizard Island, Australia. Aust. J. Mar. Freshw. Res. 38, 211–223.

Levin, P.S., 1991. Effects of microhabitat on recruitment variation in a Gulf of Maine reef fish. Mar. Ecol. Prog. Ser. 75, 183–189.

Levin, P.S., 1993. Habitat structure, conspecific presence and spatial variation in the recruitment of a temperate reef fish. Oecologia 94, 176–185.

Levin, P.S., 1994. Fine-scale temporal variation in recruitment of a temperate demersal fish: the importance of settlement versus post-settlement loss. Oecologia 97, 124–133.

Levin, P.S., 1996. Recruitment in a temperate demersal fish: does larval supply matter?. Limnol. Oceanogr. 41, 672–679.

Milicich, M.J., 1994. Dynamic coupling of reef fish replenishment and oceanographic processes. Mar. Ecol. Prog. Ser. 110, 135–144.

Milicich, M.J., Doherty, P.J., 1994. Larval supply of coral reef fish populations: magnitude and synchrony of replenishment to Lizard Island, Great Barrier Reef . Mar. Ecol. Prog. Ser. 110, 121–134.

Milicich, M.J., Meekan, M.G., Doherty, P.J., 1992. Larval supply: a good predictor of recruitment of three species of reef fish (Pomacentridae). Mar. Ecol. Prog. Ser. 86, 153–166.

Molles, M.C., 1978. Fish species diversity on model and natural reef patches: experimental insular biogeography. Ecol. Monogr. 48, 289–305.

Morris, D.W., 1987. Ecological scale and habitat use. Ecology 68, 362–369.

Munro, J.L., Williams, D.McB., 1985. Assessment and management of coral reef fisheries: biological, environmental, and socio-economic aspects. Proc. 5th Int. Coral Reef Congr. 4, 543–581.

Planes, S., Levefre, A., Legendre, P., Galzin, R., 1993. Spatio-temporal variability in fish recruitment to a coral reef (Moorea, French Polynesia). Coral Reefs 12, 105–113.

Richards, W.J., Lindeman, K.C., 1987. Recruitment dynamics of reef fishes: planktonic processes, settlement and demersal ecologies, and fishery analysis. Bull. Mar. Sci. 41, 392–410.

Russel, B.C., Anderson, G.R.V., Talbot, F.H., 1977. Seasonality and recruitment of coral reef fishes. Aust. J. Mar. Freshw. Res. 28, 521–528.

Sale, P.F., 1985. Patterns of recruitment in coral reef fishes. Proc. 5th Int. Coral Reef Congr. 5, 391–396.

Sale, P.F., 1990. Recruitment of marine species: is the bandwagon rolling in the right direction. Trends Ecol. Evol. 5, 25–27.

Sale, P.F., Douglas, W.A., Doherty, P.J., 1984. Choice of microhabitats by coral reef fishes at settlement. Coral Reefs 3, 91–99.

Sale, P.F., Doherty, P.J., Eckert, G.J., Douglas, W.A., Ferrel, D.J., 1984. Large scale spatial and temporal variation in recruitment to fish populations on coral reefs. Oecologia 64, 191–198.

Sale, P.F., Ferrel, D.J., 1988. Early survivorship of juvenile coral reef fishes. Coral Reefs 7, 117–124.

Schroeder, R.E., 1985. Recruitment rate patterns of coral-reef fishes at Midway Lagoon. Proc. 5th Int. Coral Reef Congr. 5, 379–384.

Schroeder, R.E., 1987. Effects of patch reef size and isolation on coral reef fish recruitment. Bull. Mar. Sci. 41, 441–451.

Shulman, M.J., 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. J. Exp. Mar. Biol. Ecol. 74, 85–109.

Shulman, M.J., 1985. Variability in recruitment of coral reef fishes. J. Exp. Mar. Biol. Ecol. 89, 205–219.

Shulman, M.J., 1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66, 1056–1066.

Shulman, M.J., Ogden, J.C., 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. Mar. Ecol. Prog. Ser. 39, 233–242.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. W.H. Freeman and Company, New York, 887 pp.

Sponaugle, S., Cowen, R.K., 1996. Larval supply and patterns of recruitment for two Caribbean reef fishes, *Stegastes partitus* and *Acanthurus bahianus*. Mar. Freshw. Res. 47, 433–447.

Sweatman, H., 1988. Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. J. Exp. Mar. Biol. Ecol. 124, 163–174.

Thresher, R.E., 1984. Reproduction in reef fishes. TFH Publications, Neptune City, New Jersey, 399 pp.

Tolimieri, N., 1995. Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. Oecologia 102, 52–63.

Victor, B.C., 1982. Daily otolith increments and recruitment in two coral-reef wrasses *Thalassoma bifasciatum* and *Halichoeres bivittatus*. . Mar. Biol. 71, 203–208.

Victor, B.C., 1983. Recruitment and population dynamics of a coral reef fish. Science 219, 419–420.

Victor, B.C., 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol. Monogr. 56, 145–160.

Walsh, W.J., 1985. Reef fish community dynamics on small artificial reefs: the influence of isolation, habitat structure, and biogeography. Bull. Mar. Sci. 36, 357–376.

Wellington, G.M., 1992. Habitat selection and juvenile persistence control the distribution of two closely related Caribbean damselfishes. Oecologia 90, 500–508.

Williams, D.McB., 1983. Daily, monthly and yearly variation in recruitment of a guild of coral reef fishes. Mar. Ecol. Prog. Ser. 10, 239–250.

Williams, D.McB., Sale, P.F., 1981. Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within 'One Tree Lagoon', Great Barrier Reef. . Mar. Biol. 65, 245–253.

Wolanski, E., 1994. Physical Oceanographic Processes of the Great Barrier Reef. CRC Press Inc., Florida, 234 pp.

Zar, J.H., 1984. Biostatistical Analysis. Prentice Hall, New Jersey, 718 pp.